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Redescription of the Cretaceous species *Archaeocerus uenoi* Perreau, 2019 based on synchrotron radiation micro-tomography and nano-tomography (Coleoptera, Leiodidae, Catopocerinae)

Michel Perreau[1], Iva Njunjić[2,3], Michiel D. de Groot[4,5], Warre Van Caenegem[4], Danny Haelewaters[4,6,7]

1 *Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, SU, EPHE-PSL, UA, 57 rue Cuvier, CP50 75005 Paris, France* **2** *Naturalis Biodiversity Center, Darwinweg 2, 2333 CR, Leiden, Netherlands* **3** *Taxon Expeditions, Rembrandtstraat 20, 2311VW, Leiden, Netherlands* **4** *Research Group Mycology, Department of Biology, Ghent University, 9000 Ghent, Belgium* **5** *Research Institute for Nature and Forest (INBO), 1000 Brussels, Belgium* **6** *Biology Centre of the Czech Academy of Science, Institute of Entomology, Branišovská 31, 370 05 České Budějovice, Czech Republic* **7** *Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic*

Corresponding author: Michel Perreau (michellouis.perreau@mnhn.fr)

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Abstract

The only known extinct species of the subfamily Catopocerinae (Leiodidae), *Archaaeocerus uenoi* Perreau, 2019, is redescribed. The female is described for the first time and the internal morphology (genitalia) of both sexes is described and illustrated using X-ray synchrotron micro-tomography and nano-tomography. These new observations allow a detailed description of the aedeagus, ensuring a complementary comparison with extant genera and confirming the placement of the genus *Archaeocerus* in the subfamily Catopocerinae.

Keywords

Extinct species, Myanmar amber, taxonomy, X-ray synchrotron micro-tomography, X-ray synchrotron nano-tomography

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Introduction

The subfamily Catopocerinae (Coleoptera: Leiodidae) is a small subfamily of small carrion beetles currently containing six genera and 53 described species. Three extant genera are known from North America: *Catopocerus* Motschulsky, 1870 with five species; *Glacicavicola* Westcott, 1968 with a single species; and *Pinodytes* Horn, 1880 with 42 species. One extant genus is known from Siberia: *Perkovskius* Lafer, 1989 with three species. Finally, another extant genus is known from Japan: *Muganryus* Nishikawa, 2018 with a single species.

All these species are anophthalmic and apterous and most of them are endogean (Peck 1975). One species, *Glacicavicola bathyscioides* Westcott, 1968, is troglobitic, inhabiting lava caves in the states of Idaho and Wyoming in the USA (Peck 1970, 1974, 1981). It exhibits a slender, elongated body shape (leptodiroid morphology) similar to the troglobitic species of the European tribe Leptodirini.

The sixth genus, *Archaeocerus* Perreau, 2019, is extinct and originates from the Cretaceous deposit of the Hukawng valley in northern Myanmar, dating back to ~99 Ma, that is, from the Albian/Cenomanian boundary (Cruickshank and Ko 2003; Shi et al. 2012). Unlike extant species, it has developed eyes and wings but other external characteristics are similar to endogean extant species and the size is similar to the smallest species of *Pinodytes* (Perreau 2019). The geographic distribution of genera of Catopocerinae is mapped in Fig. 1.

Few data are available on the bionomics of Catopocerinae. Except for *Glacicavicola bathyscioides*, the troglobitic species, which has been observed feeding on

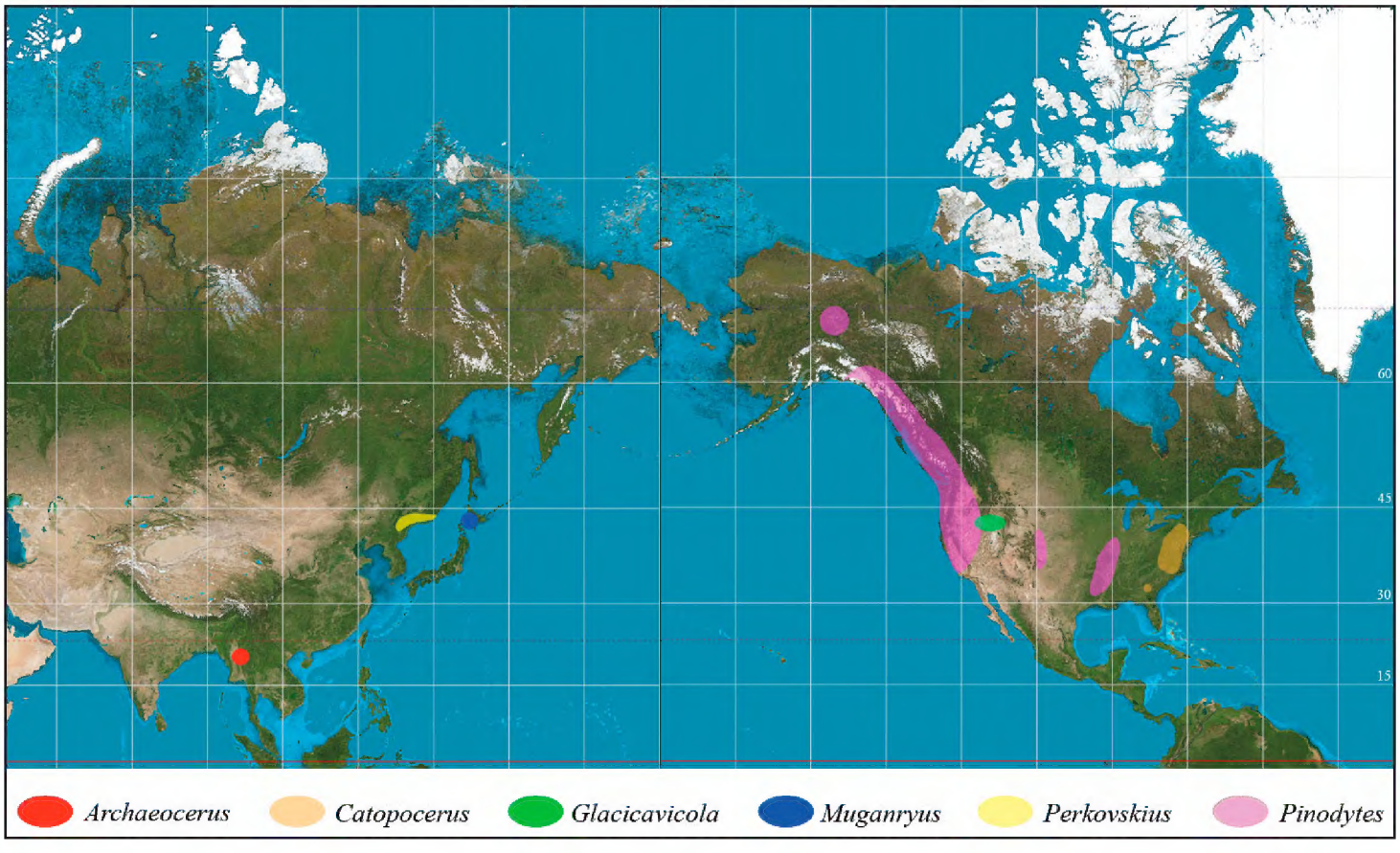


Figure 1. Distribution map of genera of Leiodidae Catopocerinae. (Background map modified from Daniel R. Strebe).

decayed arthropods both in caves and by rearing (Peck 1974), the other extant genera are at least partly mycophagous. Several *Catopocerus* species have been observed feeding from sporocarps both in the field (Fogel and Peck 1975) and by rearing (Peck 1975). In addition, fungal spores have been observed directly in the gut of *Catopocerus* spp. (Newton 1984), *Muganryus susumui* (Nishikawa 2018), and *Perkovskius zerchei* (Perreau and Růžička 2007).

This paper presents a redescription of the male holotype of the fossil species, *Archaeocerus uenoi*, using micro-tomographic and nano-tomographic observations that enable the virtual dissection of specimens in a non-destructive way (Perreau and Tafforeau 2011). Moreover, the discovery of a new specimen (deposited in the private collection of M. Perreau) allows for the description of the internal and external morphology of the female.

Methods

Synchrotron X-ray micro-tomography and nano-tomography

Propagation phase contrast micro-tomography and nano-tomography were performed at the European Synchrotron Radiation Facility (ESRF, Grenoble, France).

Phase contrast micro-tomography scans were performed on the beamline BM05 with a monochromatic X-ray beam, using a multilayer monochromator, at the energy of 29 keV and with a propagation distance of 500 mm. The scintillator was either a LSO:Tb 8.8 µm (Tb-doped Lu2SiO5) coupled to a optical microscope Peter twinmic with a × 10 lens, for the resolution 0.73 µm or a LSO:Tb 4.8 µm with a lens × 20 for the resolution 0.34 µm. The camera was a PCO edge 4.2 CLHS with a resolution of 2048 × 2048 pixels. 6000 projections were acquired over a range of 360° with an exposure time of 30 ms and a continuous rotation to blur out undesired artifacts located outside the field of interest (far from the rotation center) and to decrease their contribution to the noise of the final reconstructed slices (Lak et al. 2006). The resolution (voxel size) was 0.73 µm for the female specimen and 0.34 µm for the male specimen. In-house software packages present at ESRF were used for tomographic reconstructions.

X-ray synchrotron nano-tomographic scans were performed on the beamline ID16B (Martínez-Criado et al. 2016) using a pink X-ray beam ($\Delta E/E=10^{-2}$) with an energy of 29.1 keV. The technique used was holotomography (Cloetens et al. 1999); each holotomographic acquisition consists of four tomographic scans slightly changing the propagation distance. For each tomographic scan, 3203 projections were acquired over 360° with an exposure time of 18 ms and a voxel size of 60 nm. The camera was a PCO edge 5.5 Cmos camera equiped with an optical microscope with a × 10 lens and a LSO:Tb 17 µm scintillator. The phase retrievial calculation was performed using in-house octave code with a CTF (contrast transfer function) algorithm and the reconstructions were performed using PyHST2 software with a filtered back projection algorithm (Mirone et al. 2014).

Data processing

Segmentations were done with VGSTUDIOMAX 3.4 (Volumegraphics, Heidelberg, Germany), the last version of the software allowing a 3D stereo–perspective processing. Raw data of the experiments are available in the ESRF Data Portal under a CC BY 4.0 license: https://doi.org/10.15151/ESRF-ES-409937097 (for micro-tomography) and https://doi.org/10.15151/ESRF-ES-652447868 (for nano-tomography).

Illustrations

Visible light pictures were taken with a keyence VHX5000 microscope and a VH-Z250T lens. Some micro-tomography and nano-tomography pictures are presented in two versions, one flat and one in 3D stereo-anaglyphes that may be visualized with red/cyan glasses. These pictures are labeled with their number followed by «a» (flat version) or «b» (3D version).

Taxonomy

Arthropoda von Siebold, 1848
Insecta Linnaeus, 1758
Coleoptera Linnaeus, 1758
Staphylinoidea Latreille, 1802
Leiodidae Fleming, 1821
Catopocerinae Hatch, 1927
***Archaeocerus* Perreau, 2019**

***Archaeocerus uenoi* Perreau, 2019**

Description. Length: 1.2 mm (male) or 1.5 mm (female). Body elongate (Figs 2, 3), flattened (Fig. 4), dark brown; antennae, legs, and mouthparts light brown.

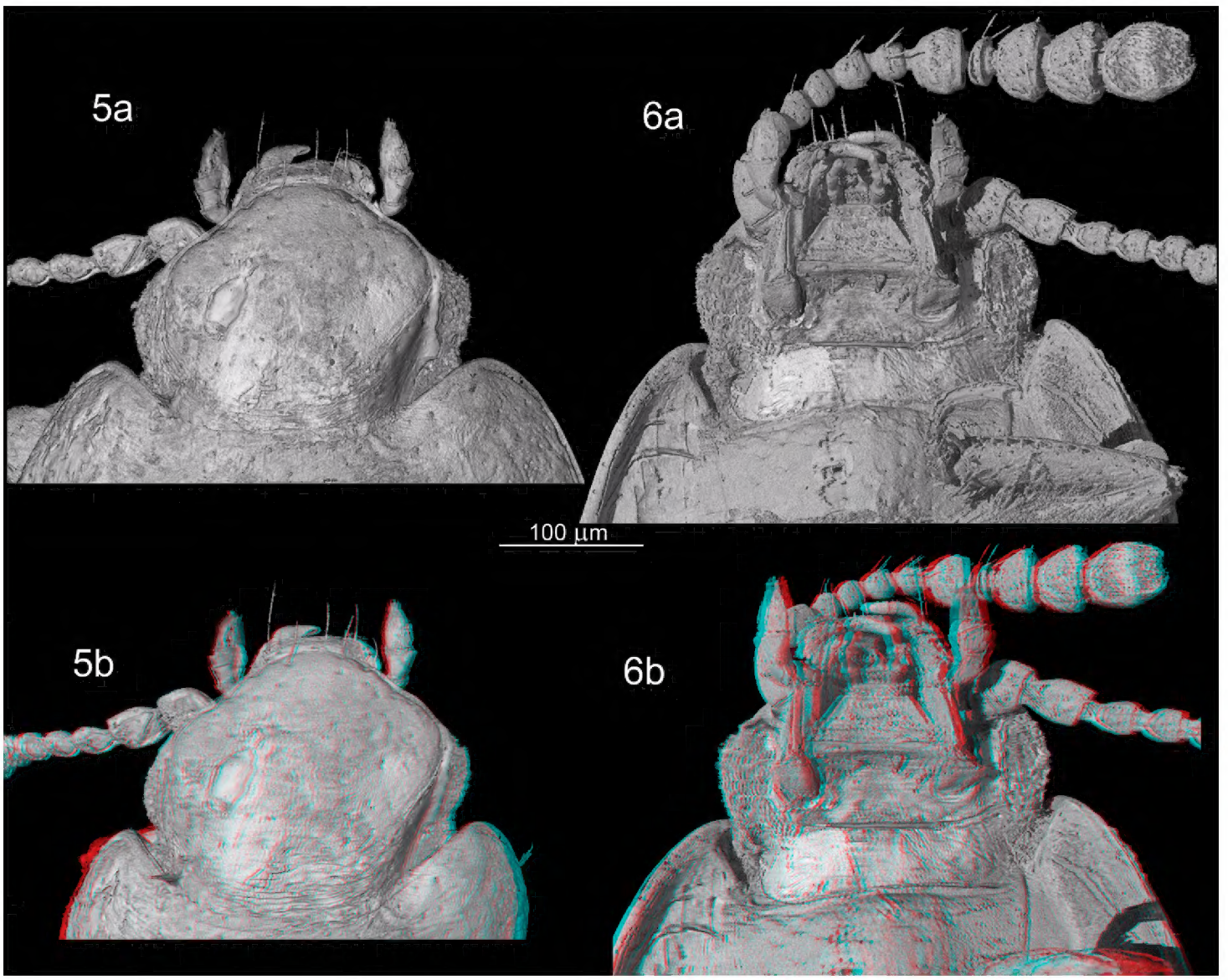
Head. Antennal insertions concealed in dorsal view (Fig. 5). Epistomal suture, epistomal stem missing, microreticulation if any, indistinct (Fig. 5). Antennae with 11 antennomeres, 8th antennomere extremely flat and significantly narrower than 7th, 9th, and 10th, without teeth (Fig. 6). Gular sutures shallow but widely distant. Pronotum transverse, approximately 1.4 × as wide as long, widest very close to the base, with sides regularly arcuate and convergent anteriorly (Fig. 2). Surface shiny, with tiny punctures and fine microreticulation, without transverse strigae (Fig. 2). Lateral margins with distinct gutter (Fig. 2).

Elytra approximately 1.4 × as long as wide jointly, parallel in the two basal third of their length, then regularly rounded at apex. A single parasutural longitudinal stria. Puncture transversely aligned in oblique strigae and associated with short setae (Fig. 2). Surface shiny, with no visible microreticulation. Marginal gutter fairly wide (Fig. 2).

Figures 2–4. *Archaeocerus uenoi*, holotype, habitus **2** dorsal view **3** ventral view **4** lateral view.

Flight wings present and probably functional, with nervation present near the base, reduced on the apical half and with numerous microtrichia and with ciliate margins.

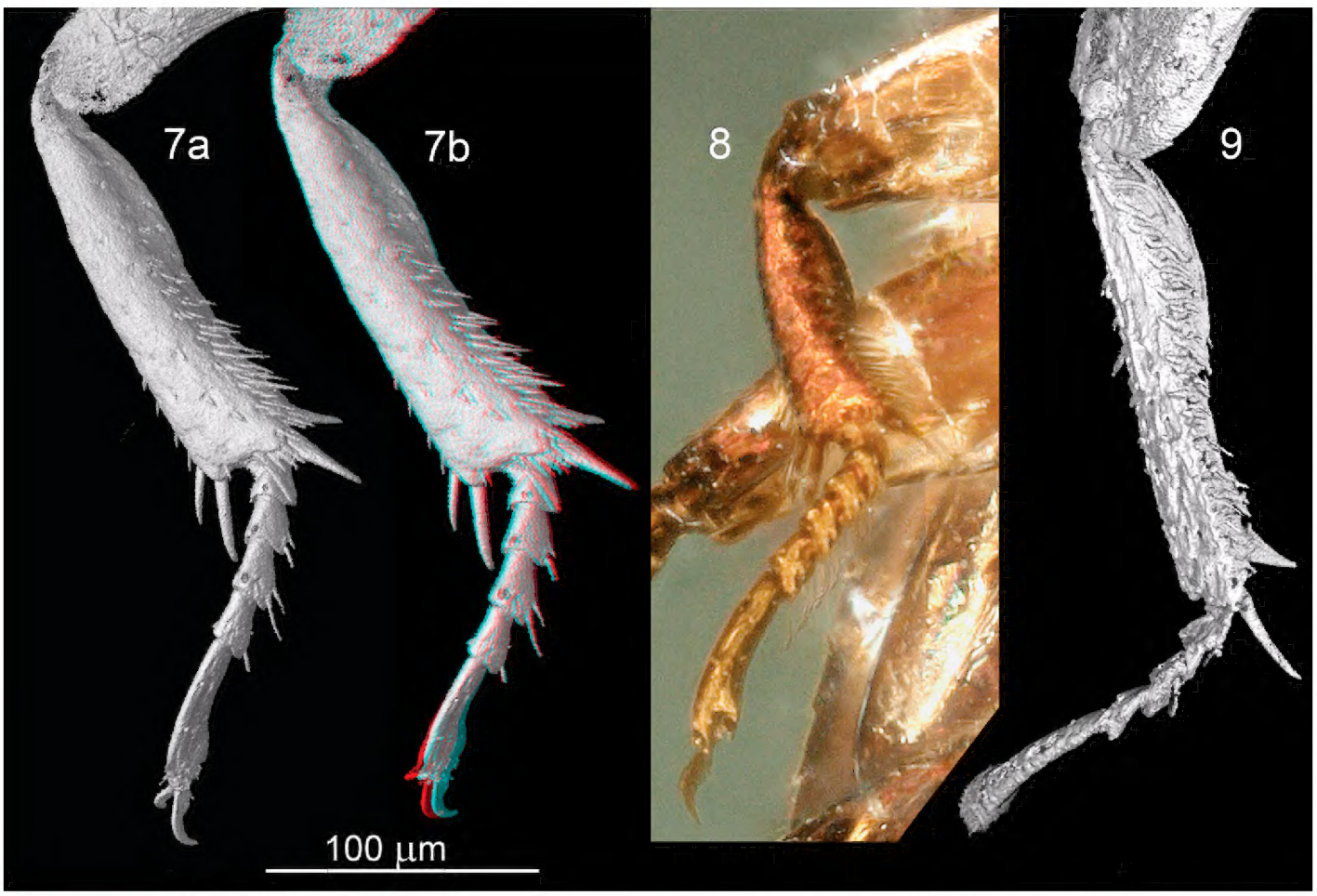
Ventral structures. Anterior part of prosternal surface elongated in front of procoxae (Fig. 2). Mesoventrum with sharp and uninterrupted longitudinal median carina. Metaventrum not carinate, but with wide medial depression located on top of a medial bulge (as the crater of a volcano). Metaventrite and first abdominal ventrite without setose paired impressions (white spots visible on the ventral surface on Fig. 2 are air bubbles, not setose impressions, without setae). Metacoxae clearly separate.



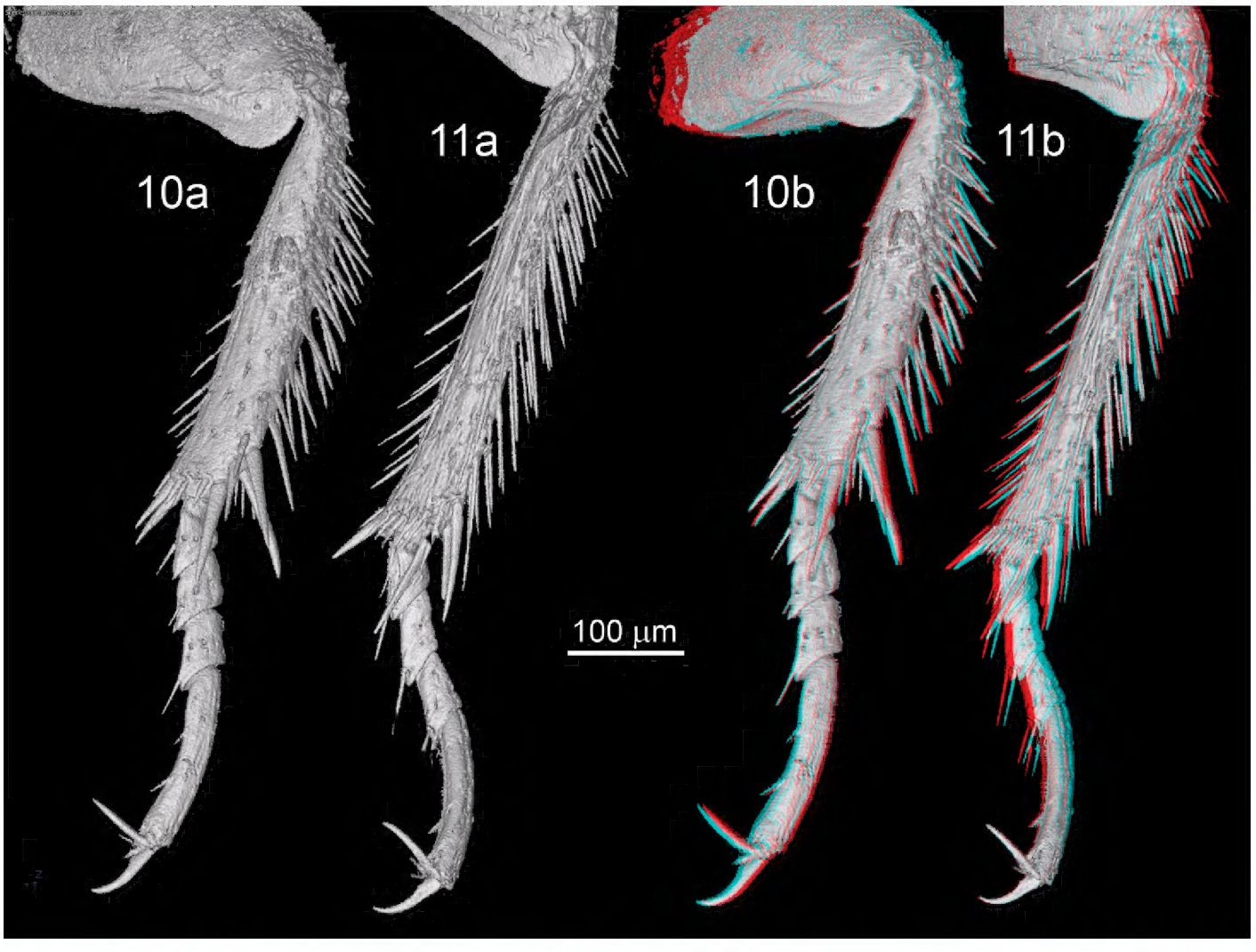
Figures 5, 6. *Archaeocerus uenoi*, holotype, head **5** dorsal view **6** ventral view. Voxel size: 0.34 µm.

Legs. Tarsal formula 5-4-4 in both sexes (Figs 7–11). Female protarsi undilated. Male protarsi imperceptibly dilated, with tenent setae of two kinds on ventral side: some very long and straight, some others shorter, curved and slightly dilated at apex (Fig. 8). Their weak contrast in X-rays does not allow visualizing them clearly in microtomography. Meso- and metatarsi undilated and without tenent setae in both sexes (Figs 10, 11). Last protarsomere as long as the four preceding ones taken together, last meso- and metatarsomeres as long as the three preceding ones taken together (Figs 10, 11). No measurable sexual differences in the relative length of tarsomeres. All tarsi with two interongular setae. Protibias thickened in basal half, bearing in both sexes an area lined with dense bunch of setae on inner margin of apical half (Figs 7–9). Outer side of protibias spineless, outer side of meso- and metatibias with strong spines (Figs 10, 11).

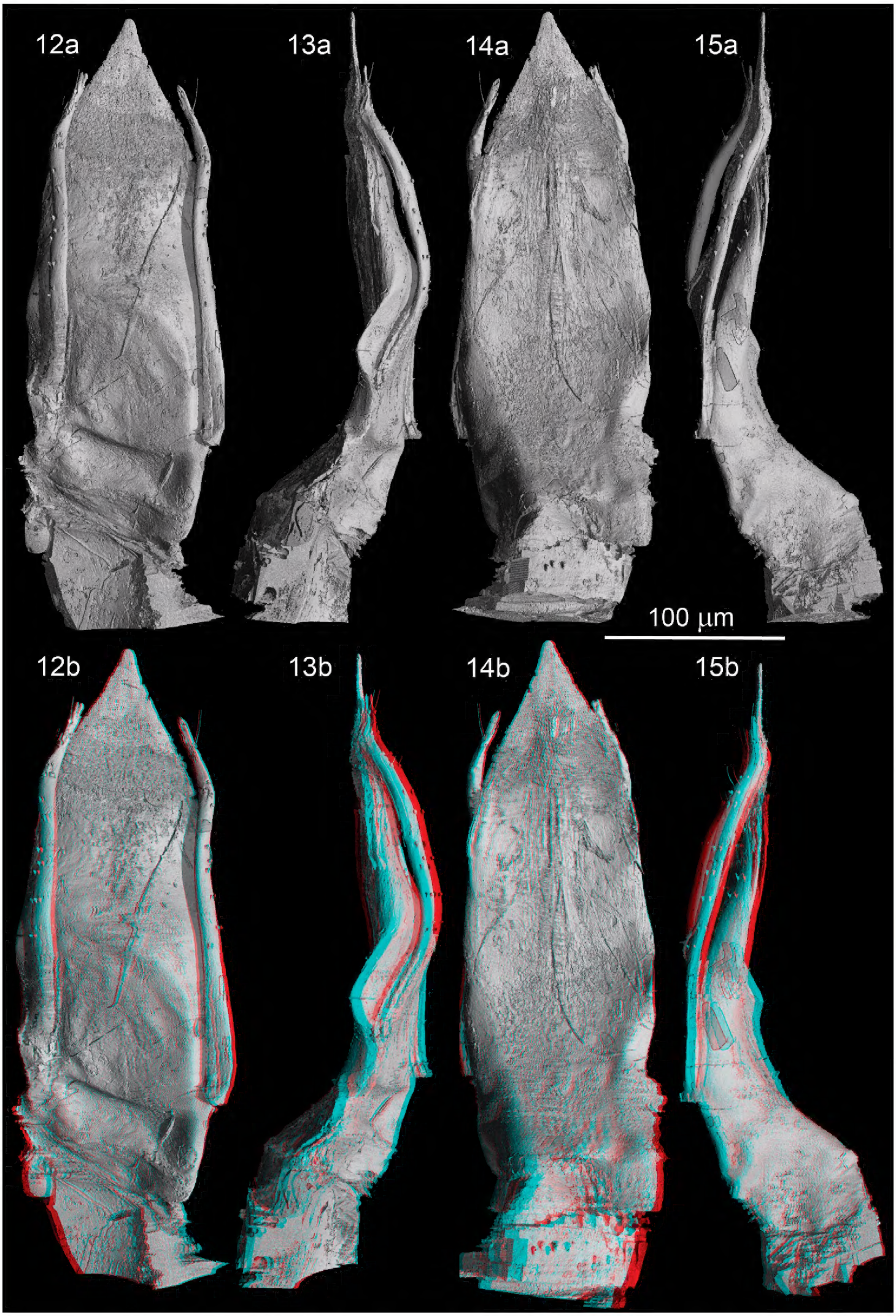
Aedeagus parallel in two basal thirds then triangularly pointing at the apex in dorsal or ventral view (Figs 12, 14), flat in lateral view (Figs 13, 15). Probably due to the poor state of preservation, the base of the median lobe and of the tegmen is not accurately resolved so that the basal orifice is not visible and the whole median lobe is not exactly symmetrical, slightly deformed. Parameres slightly shorter than the median lobe (Figs 12–14), with two subapical distant setae, distal one on the outer side, proximal one on dorsal side (Fig. 19). Parameres seemingly disconnected from indistinct basal part of tegmen. Endophallus with wide basal structure with two lateral expansions (Fig. 18) and long stylus, roughly cylindrical,



Figures 7–9. *Archaeocerus uenoi*, anterior legs **7a, b, 8** right male protibia (holotype), ventro-lateral view **9** right female protibia, ventro-lateral view. Voxel size: 0.34 µm (Fig. 7); 0.73 µm (Fig. 9).



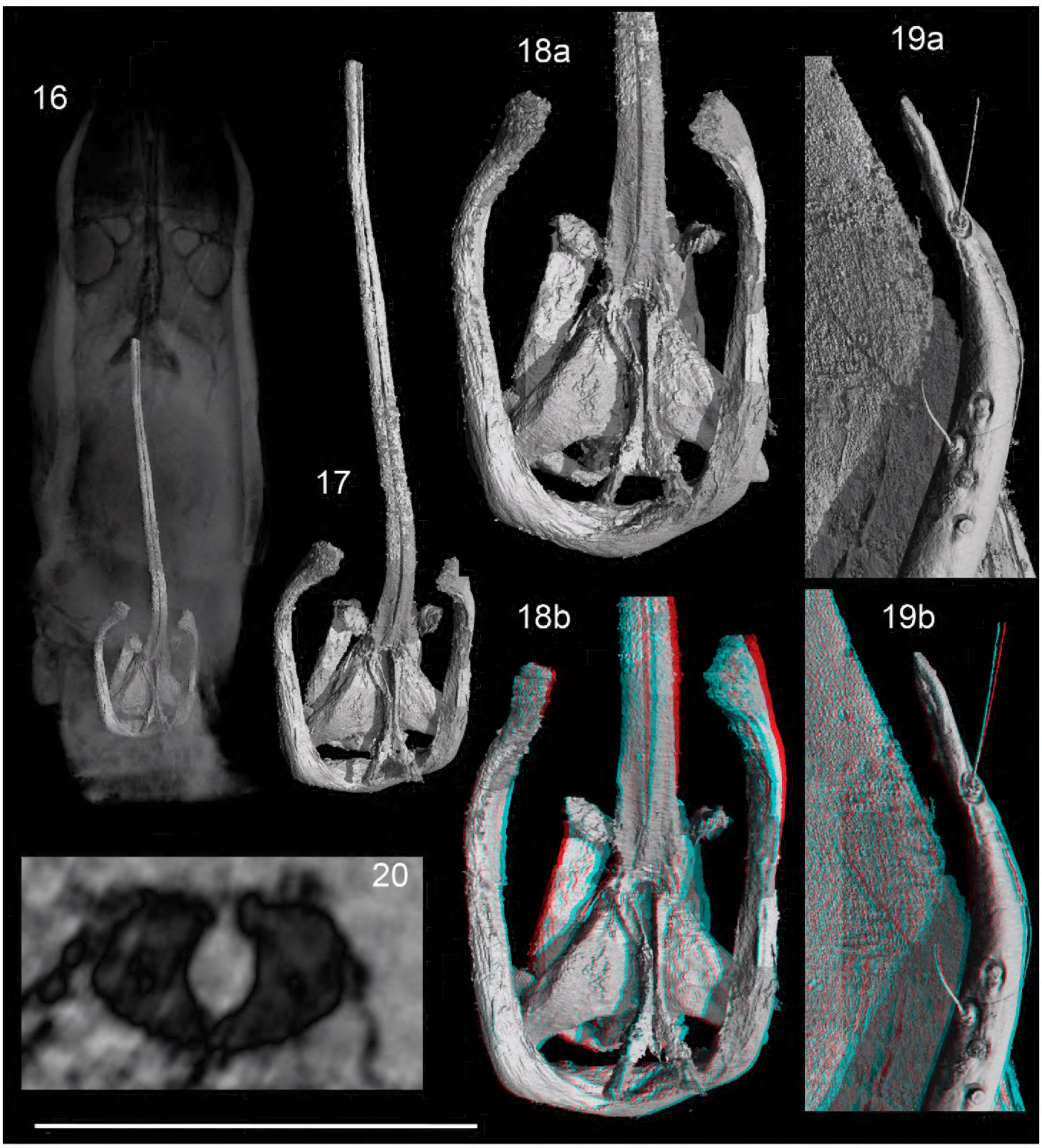
Figures 10, 11. *Archaeocerus uenoi*, holotype **10a, b** left mesotibia and mesotarse, ventral view **11a, b** left metatibia and metatarse, ventral view. Voxel size: 0.34 µm.



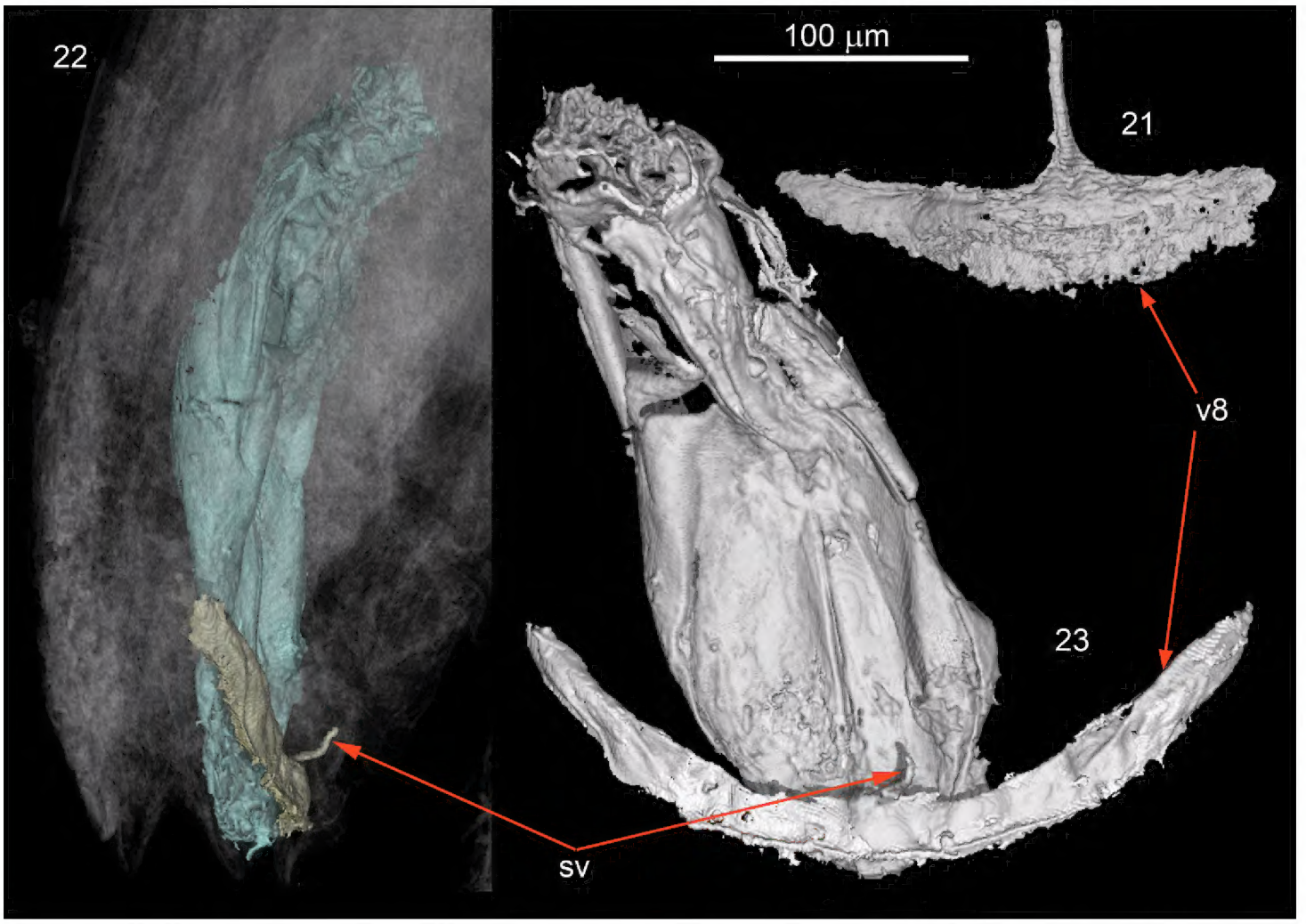
Figures 12–15. *Archaeocerus uenoi*, holotype, aedeagus **12a, b** dorsal view **13a, b** right lateral view **14a, b** ventral view **15a, b** left lateral view. Voxel size: 0.06 µm.

not closed on the dorsal side, with more or less gutter shape (Figs 16, 17). A transversal cut taken from one slice of the nano-tomographic reconstruction is shown on Fig. 20. Flat and 3D videos of the aedeagus including the endophallus are given in Suppl. materials 1, 2.

Ventrite VIII male and female both with *spiculum ventrale* (Figs 21–23). Male genital segment only partly distinct, making impossible to determine its general morphology. Female genital segment as in Figs 22, 23. It is impossible to determine if the lack of visible appendicular parts in the female genital segment and the indistinct male genital segment are an actual depletion or reduction or if it results from the poor state of preservation.



Figures 16–20. *Archaeocerus uenoi*, holotype, aedeagus **16a, b** aedeagus dorsal view with transparency showing the endophallus **17** endophallus **18a, b** base of the endophallus **19a, b** apex of the parameres **20** transversal slice of the reconstruction at the level of the ductus of the endophallus. Scale bars: 200 μm (**16**); 100 μm (**17**); 50 μm (**19**); 40 μm (**18**); 10 μm (**20**). Voxel size: 0.06 μm.



Figures 21–23. *Archaeocerus uenoi*, genital structures **21** male ventrite VIII **22** female ventrite VIII and abdominal segment IX, lateral view, with different colors for clarity and abdomen in transparency **23** female ventrite VIII and segment IX, ventral view. v8=ventrite VIII, sv=*spiculum ventrale*. Pictures from micro-tomography. Voxel size: 0.34 µm (Fig. 21); 0.73 µm (Figs 22, 23).

Discussion

The subfamily Catopocerinae is one of the two subfamiles of Leiodidae found as monophyletic in McKenna et al. (2015). *Archaeocerus* shares all characteristics defining the subfamily: (i) the invagination of the abdominal segment VIII inside the abdomen, leading to five visible abdominal coxosternites instead of six in most of Leiodidae (Newton et al. 2016); (ii) the prosternum longer than the coxal width, and (iii) the genital structures, especially the presence of a *spiculum ventrale* in both sexes. Differences with the other genera are as follows: presence of developed eyes and wings (versus all extant species anophthalmic and apterous) and tarsal formula 5-4-4 in both sexes (versus 5-5-5 in the other genera except *Perkovskius* 5-5-3 in males and 4-4-3 in females).

Other characteristics important for the phylogeny of Catopocerinae (Peck and Cook 2011) are the following:

i. The apical setae of parameres are distant and in a dorso-lateral position as in the genera *Muganryus*, *Perkovskius*, and a few species of *Pinodytes* of the «pusio» species group (Peck and Cook 2011). They are apical and contiguous in *Glacicavicola* and most of species of *Pinodytes*. They are completely missing in *Catopocerus*.

ii. The endophallus of *A. uenoi*, with a long gutter-shaped stylus and a basal symmetric structure, is significantly different from what is observed in extant genera of Catopocerinae. Some species of *Pinodytes* have no internal sclerotized structure in the endophallus, others have sets of numerous spines, teeth or setae (Peck and Cook 2011). In *Muganryus*, spines and shallow sclerites are located at the base of the endophallus (Nishikawa 2018) and in *Glacicavicola*, the endophallus is unarmed. A complex basal structure is observed in *Perkovskius* (Perreau and Růžička 2007), in some way similar to that of *Archaeocerus*. But no extant genus shows a long tubular stylus as in *Archaeocerus*. The internal structures of the endophallus of *Archaeoceus* looks more like the Y-shaped basal piece in Leptodirini (Cholevinae) which also extends with a long stylus. However, it has never been observed that the stylus of Leptodirini is tubular. An internal stylus is observed also in Ptomaphagini (Cholevinae) but it has no dorsal longitudinal opening. However, the few accurate illustrations available by scanning electron microscopy show some kind of aperture at the apex, suggesting an internal void in several species of the genus *Adelopsis* Portevin, 1907 (Gnaspini and Gomyde 2025).

In conclusion, *Archaeocerus* shows a mixing of plesiomorphic character states (lack of eyes and wings) and of presumably apomorphic characteristics: tarsal formula, complex basal structure of the endophallus. It might be tempting to consider it the sister group of all extant genera, but this remain speculative in the absence of a comprehensive phylogenetic analysis of the extant genera.

The identification table of genera of Catopocerinae can be updated from Perreau (2019) as follows:

1 Eyes and flight wings present. Epistomal suture and median stem indistinct. Tarsal formula 5-4-4 in both sexes. Extinct species..... ***Archaeocerus* Perreau, 2019**

– Eyes and flight wings absent. Epistomal suture distinct. Tarsal formula not 5-4-4. Extant species..... **2**

2 Tarsal formula 5-5-5 in both sexes **3**

– Tarsal formula 5-5-3 (male) or 4-4-3 (female)..... ***Perkovskius* Lafer, 1989**

3 Gular sutures confluent. Epistomal suture without median stem. Pronotum without lateral margins. Leptodiroid body shape ..... ***Glacicavicola* Westcott, 1968**

– Gular sutures distant. Epistomal suture with median stem. Pronotum with lateral margins. Bathyscioid body shape..... **4**

4 Both mesoventrite and metaventrite with longitudinal median carina..... **5**

– Mesoventrite with longitudinal median carina, metaventrite not carinate ..... ***Muganryus* Nishikawa, 2018**

5 Antennomeres VII, IX, and X bearing several teeth. Metaventrite and first visible abdominal ventrite with setose paired impressions. *Spiculum gastrale* absent from male abdominal segment IX and *spiculum ventrale* absent

from female abdominal ventrite VIII. Parameres separate from basal piece of tegmen..... ***Catopocerus* Motschulsky, 1870**

– Antennomeres VII, IX, and X without teeth. Metaventrite and first visible abdominal ventrite without setose paired impressions. *Spiculum gastrale* present in male abdominal segment IX and *spiculum ventrale* present on female abdominal ventrite VIII. Parameres continuous with basal piece of tegmen .. .. ***Pinodytes* Horn, 1880**

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Supplementary material 1

***Archaeocerus uenoi*: Video of the aedeagus and endophallus in rotation (flat version)**

Authors: Michel Perreau, Iva Njunjić, Michiel D. de Groot, Warre Van Caenegem, Danny Haelewaters

Data type: mp4

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Link: https://doi.org/10.3897/subtbiol.52.154293.suppl1

Supplementary material 2

***Archaeocerus uenoi*: Video of the aedeagus and endophallus in rotation (3d version)**

Authors: Michel Perreau, Iva Njunjić, Michiel D. de Groot, Warre Van Caenegem, Danny Haelewaters

Data type: mp4

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